

A QUANTITATIVE EVALUATION OF INTRASPECIFIC AND  
INTERSPECIFIC VARIATION IN EYE MORPHOLOGY FOR *EFFERIA*  
COQUILLET (DIPTERA: ASILIDAE) SPECIES

K. C. HOLSTON AND C. R. NELSON

(KCH) Swedish Museum of Natural History, Section for Entomology, P.O. Box 50007, S-104 05 Stockholm, Sweden (e-mail: kevin.holston@nrm.se); (CRN) Department of Integrative Biology, WIDB 401, Brigham Young University, Provo, UT 84602, U.S.A. (e-mail: rileynelson@byu.edu).

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*Abstract.*—Qualitative taxonomic characters based on differences in linear eye measurements were converted to qualitative scores for *Efferia* group species, and statistical analyses of intraspecific and interspecific variation were performed. Sexual dimorphism noted for *E. albibarbis* is the first documented for an eye morphology character in Asilidae, and may be analogous to sexual dimorphism described in a holoptic-dichoptic context for other species of Diptera. Interspecific variation in *E. albibarbis* Macquart and *E. aestuans* (Linnaeus) demonstrates that robust comparisons among species cannot rely on single exemplars, and differences among specimens based on sex and geography should be considered during subsequent eye morphology studies in Asilidae. The variables identified in this study demonstrate that a wide variation in eye morphology exists among *Efferia* group species that can be examined in a quantitative context. Detailed accounts of intraspecific variation are considered crucial for comparisons among species of Asilidae, and interspecific comparisons of eye morphology are likely to demonstrate biologically significant results in studies of monophyletic taxa and ecological guilds.

*Key Words:* intraspecific variation, eye morphology, robber fly, *Efferia albibarbis*, *Efferia aestuans*

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Compound eyes of robber flies (Diptera: Asiloidea: Asilidae) are sensory organs of great importance for these active visual predators, and studies of eye morphology are relevant to further taxonomic, ecological, and phylogenetic assessments of Asilidae. Robber flies hunt primarily from exposed perches on vegetation or the ground, where they often move their heads and reorient their bodies in response to movements of potential prey. The subsequent attack flight has been described as “target-directed” or “ballistic interception” (Buschbeck and Strausfeld 1996, 1997), and differences among species have been

noted concerning hovering ability, habitat preferences, and prey handling. The compound eyes of robber flies are large and prominent with respect to dorsal and ventral margins of the head in anterior view, such that the vertex appears “excavated” (Wood 1981, Lehr 1988, Majer 1997). Eyes in both sexes are well-separated at the vertex (Wood 1981), which has been considered an evolutionarily derived characteristic for Asilidae (Yeates 1994), although holoptic males (i.e., the margins of the compound eyes meet dorsally at vertex) and dichoptic females (i.e., compound eyes separated) frequently characterize species of Diptera

(McAlpine 1981). The predatory behavior of robber flies may promote similar eye morphology between males and females, but sexual dimorphism has been noted for other body parts directly involved with predation, such as wings and legs (Hull 1962, Lavigne 2002).

Intraspecific differences in eye morphology, however, have not been documented, and interspecific differences are generally summarized as qualitative taxonomic characters to differentiate among genera. The degree to which the compound eyes converge toward the vertex is often used in taxonomic characterizations of Asilidae, with the vertex width relative to face width used to distinguish genera having compound eyes that are widely divergent towards the vertex (e.g., *Stichopogon*, *Lasiopogon*, *Townsendia*, *Willistonina*) (Wood 1981). Quantitative variables for eye morphology would facilitate precise comparisons among specimens and species and allow eye morphology to be incorporated in biological investigations of robber fly species.

The wide geographical distribution and abundance of *Efferia albibarbis* (Macquart), and its distinctive eye morphology makes this species an appropriate choice for describing intraspecific variation in *Efferia*. Fisher and Hespeneide (1992) considered *E. albibarbis* the most common robber fly in North and Central America, and this species is often well represented in collections of North American Asilidae. Wilcox (1966) noted in his key to the "Albibarbis Group" that *E. albibarbis* has a "frons at vertex as wide as at antennae" in contrast to the narrower vertex in other Albibarbis Group species. Wilcox (1966) also reported eye, face, and vertex widths for 81 Nearctic *Efferia* species, but the utility of these measurements in taxonomic or biological studies has not been evaluated. *Efferia aestuans* (Linnaeus) is a North American species that is also well represented in collections, and a comparison of eye morphology among *Efferia* species with emphasis on intraspecific variation in *E. albibarbis* and *E. aestuans*

would provide an informative reference for further studies.

Face, eye, and vertex widths have been reported in descriptions of robber fly species and can be expressed as ratios that describe the relative proportions of these measurements. Qualitative taxonomic diagnostic characters used in keys, such as "face wide, about width of eye" or "frons greatly expanded toward vertex" are based on the relative widths of these three features (Wood 1981). The distance between the compound eyes across the face ("face width") and across the vertex ("vertex width") and the width of the eye are measured from endpoints on the eye margin; these measurements describe, therefore, three major aspects of the anterior eye morphology. Ratios derived from these linear measurements yield values corresponding directly to these taxonomic characters that eliminate the effect of specimen size from comparisons. For example, if face and eye width are equal, then the 1:1 ratio can be expressed as the quotient of face width/eye width, or 1.0; a 1:2 ratio for a specimen with eye width twice that of the face yields a value of 0.5.

In this study, interspecific and intraspecific differences in relative face, eye, and vertex widths for Nearctic *Efferia* species were examined to evaluate the utility of eye measurements in a quantitative context.

#### MATERIALS AND METHODS

**Nomenclature.**—Although the Nearctic *Efferia* species featured in this study have been divided recently among seven genera, these genera represent groups of *Efferia* species considered artificial groups by previous authors (Hine 1919, Wilcox 1966, Martin and Papavero 1970, Fisher and Hespeneide 1992, Artigas and Papavero 1997). Name combinations for species correspond to the genus level classification of Asilidae by Fisher and Hespeneide (1992) such that all species names are presented in combination with *Efferia* except *Triorla interrupta* (Macquart). The genus names re-

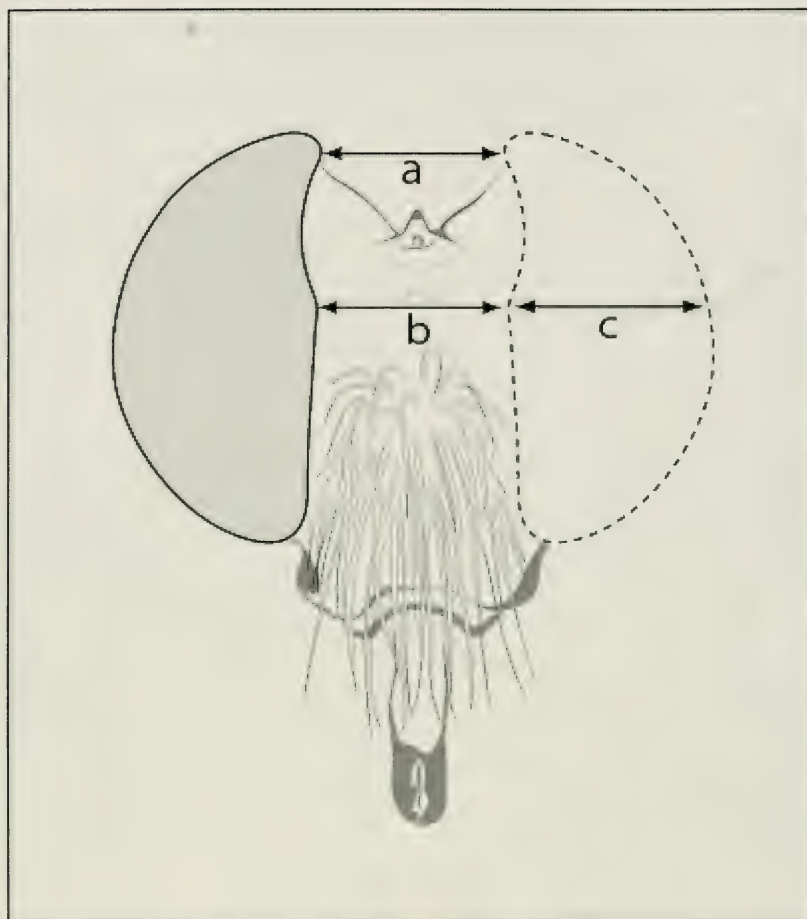


Fig. 1. Diagram of a robber fly head (*E. albibarbis*, anterior view with antennae and upper setae of head removed), showing the three distances measured (a = width of vertex, b = width of face, c = width of left eye).

cently proposed for *Efferia* species groups or removed from synonymy with *Efferia* by Artigas and Papavero (1997) are not used. The term “*Efferia* group species” is used, therefore, in reference to the Nearctic *Efferia* species plus *T. interrupta*. Names and circumscriptions for species groups in *Efferia* follow Wilcox (1966) except that *T. interrupta* is considered separately from *Efferia* and *Staminea* group species.

Eye morphology measurements.—Measurements for the left compound eye, face, and vertex widths were recorded for 103 specimens of *E. albibarbis* and 48 specimens of *E. aestuans* housed at the Illinois

Natural History Survey (INHS) (Fig. 1). Localities from which specimens were collected were grouped by geographic area: 1) Midwestern United States (MWUSA), 2) Baja California Norte, Mexico (BAJA), 3) Central America (CAMER), and 4) southwestern United States (SWUSA), (Table 1). Measurements of the head in anterior view were recorded using an ocular micrometer at 50 $\times$  and are reported as ocular micrometer units (*omu*).

Wilcox (1966) reported measurements of the eye, face, and vertex for 81 Nearctic *Efferia* group species in ocular micrometer units at a magnification of “about 30

Table 1. Localities from which specimens of *E. aestuans* and *E. albibarbis* were examined, grouped by the geographic region noted for comparisons. Legend: MWUSA = midwestern USA. SEUSA = southeastern USA. SWUSA = southwestern USA. CAMER = Central America, BAJA = Mexico, Baja California Norte.

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MWUSA	Indiana (Clinton), Illinois (Adams, Bond, Brown, Champaign, Dubois, Eddyville, Edgar, Effingham, Hancock, Iroquois, Jackson, Marion, McHenry, McLean, Pope, Pulaski, Richland, Scott, St. Clair, Wabash), Michigan (Berriens).
SWUSA	Arizona (Mohave, Pima, Santa Cruz), New Mexico (McKinney, Otero).
CAMER	Guatemala (Esquintla, Quiche), El Salvador (Cajunte), Costa Rica (Guanacaste, Puntarenas).
BAJA	Baja California Norte.

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times.” Measurements were recorded for a single male specimen of most species; a female was measured for *E. femorata* (Macquart) and *E. clementi* (Wilcox and Martin).

Eye morphology variables.—We have used four variables to compare differences in eye morphology among specimens, using ratios derived from linear measurements to control for differences in specimen size. A straightforward quantitative description of eye convergence toward the vertex is the face width across the antennal bases divided by the vertex width (*face/vertex*). An additional description of eye convergence is obtained by subtracting the face width divided by eye width (*face/eye*) from the vertex width divided by eye width (*vertex/eye*). This “*Convergence-Divergence Index*” (CDI) is distinguished from *face/vertex* by its use of two variables that incorporate eye width ( $CDI = face/eye - vertex/eye$ ). Scores showing low or no variability within and strong differences among groups indicate variables that are most appropriate for taxonomy.

Proportional change in eye morphology.—The relationship between *face/vertex* and CDI scores allows correlation plots to depict proportional changes in eye width among specimens examined, which allows the variables describing eye convergence to

be evaluated based on predicted patterns. Differences in eye width determine the range of variation in CDI scores and the placement and spread of observations in correlation plots.

*Pattern 1:* If face, vertex, and eye width measurements are constant or proportional among specimens, then *face/vertex* and CDI scores will be identical and all observations share a single point in the correlation plot.

*Pattern 2:* If only eye width varies and face and vertex widths are constant or proportional among specimens, then *face/vertex* scores will be identical and the distribution of observations is linear and perpendicular to the x-axis.

*Pattern 3:* If eye width is constant and face and vertex widths increase arithmetically (e.g., face and vertex increase by 2 *omu*), then CDI scores will be identical and the distribution of observations is linear and perpendicular to the y-axis. This pattern also characterizes groups with identical differences in *face/eye* and *vertex/eye* scores.

*Pattern 4:* If vertex and eye widths are constant or proportional and only face width varies, then the distribution can be described by the following linear equation:  $y = (vertex/eye)x - (vertex/eye)$ . The slope of this line is  $m = vertex/eye$ , the y-intercept is  $b = -vertex/eye$ , and the x-intercept is at (1,0). “*Pattern 4*” also characterizes groups of specimens having arithmetic increases in face, vertex, and eye widths. Distributions become more curvilinear as eye measurements change in larger increments, and the closest fits are expected for small incremental increases.

An additional characteristic of *face/vertex* and CDI correlation should be noted. The point indicating equal face and vertex widths is (1, 0), where the *face/vertex* score equals 1 and the CDI equals 0. As the widths of the face and vertex become increasingly similar (e.g., *face/vertex* → 1), differences in CDI scores for an identical range of eye widths are smaller due to closer *face/eye* and *vertex/eye* scores near the x-intercept. The fit of observations in a *face/*

*vertex* and CDI correlation plot to the linear equations described above would be closer near the x-intercept even when overall variation in eye width does not change.

Statistical descriptions and analyses.—Box plots were constructed to summarize descriptive statistics for *Efferia* group species, with inner fences for the data extending 1 step beyond the interquartile range. Correlation plots were developed to describe the relationship between the *face/vertex* ratio and CDI, with linear regressions calculated in Microsoft® Excel 2000, version 9.0. Pairwise comparisons between groups of specimens measured during this study (separated by species, geographic region, and sex) were performed using unpaired two-tailed *t*-tests. These comparisons test for significant differences in eye morphology scores between *E. albibarbis* and *E. aestuans* and between conspecific males and females.

## RESULTS

Intraspecific variation.—In *E. aestuans*, there is a higher correlation between face and vertex widths in males ( $y = 0.6901x + 8.6234$ ,  $R^2 = 0.8902$ ) than females ( $y = 0.6956x + 8.0324$ ,  $R^2 = 0.8879$ ), a lower correlation in face and eye for males ( $y = 1.4152x + 11.518$ ,  $R^2 = 0.6644$ ) than females ( $y = 1.4298x + 13.858$ ,  $R^2 = 0.8420$ ), and a lower correlation in vertex and eye widths in males ( $y = 0.3046x + 26.632$ ,  $R^2 = 0.5230$ ) than females ( $y = 0.4063x + 19.776$ ,  $R^2 = 0.7354$ ). In *E. albibarbis*, there is a lower correlation between face and vertex widths in males ( $y = 0.9942x + 1.4494$ ,  $R^2 = 0.6968$ ) than females ( $y = 0.8615x + 7.6243$ ,  $R^2 = 0.9048$ ), a higher correlation in face and eye for males ( $y = 1.1037x + 1.9346$ ,  $R^2 = 0.7584$ ) than females ( $y = 0.7326x + 17.986$ ,  $R^2 = 0.4741$ ), and a higher correlation in vertex and eye widths in males ( $y = 0.7171x + 14.957$ ,  $R^2 = 0.5824$ ) than females ( $y = 0.5417x + 25.768$ ,  $R^2 = 0.3931$ ).

Intraspecific variation in *E. aestuans* and

*E. albibarbis* indicate moderate levels of variation in the variables studied, with no overlap in *face/vertex* and CDI scores (Table 2). The *face/vertex* and CDI scores are higher for *E. aestuans* than for *E. albibarbis*, showing that the compound eyes in *E. aestuans* (*face/vertex*: 1.1020 to 1.2745, mean =  $1.1910 \pm 0.0408$ ; CDI: 0.0806 to 0.1872, mean =  $0.1326 \pm 0.0241$ ) converge more strongly towards the vertex than for *E. albibarbis* (*face/vertex*: 0.8841 to 1.0526, mean =  $0.9745 \pm 0.0434$ ; CDI:  $-0.1228$  to 0.0476, mean =  $-0.0242 \pm 0.0413$ ). The *face/eye* and *vertex/eye* scores show that eye width is generally greater than face or vertex widths in both *E. aestuans* (*face/eye*: 0.7037 to 0.9643, mean =  $0.8345 \pm 0.0531$ ; *vertex/eye*: 0.5977 to 0.8750, mean =  $0.7019 \pm 0.0576$ ) and *E. albibarbis* (*face/eye*: 0.7746 to 1.0678, mean =  $0.9011 \pm 0.0642$ ; *vertex/eye*: 0.8060 to 1.0702, mean =  $0.9225 \pm 0.0620$ ) and that *E. albibarbis* has more similar face, vertex and eye widths.

The linear relationship between *face/eye* and CDI scores indicates a trend toward proportional change in eye measurements for *E. albibarbis* and *E. aestuans* following the "Pattern 4" distribution, but variation in scores shows that increases are arithmetic (Fig. 2). The distribution for all *E. albibarbis* specimens can be described by a linear regression ( $y = 0.9548x - 0.9547$ ,  $R^2 = 0.9941$ ) with a slope similar to the observed mean ( $0.9547 \pm 0.0513$ ) and median (0.9547) *vertex/eye* scores. Similarly, the distribution for *E. aestuans* can be described by a linear regression ( $y = 0.6987x - 0.7$ ,  $R^2 = 0.8225$ ) close to the observed mean ( $0.7019 \pm 0.0576$ ) and median (0.6992) *vertex/eye* scores. The correlation plot for *face/eye* and CDI shows lower fit to a linear regression for *E. aestuans* than for *E. albibarbis* although higher standard deviations are observed for *E. albibarbis*, which is predicted from the calculation of the CDI for distributions closer to the x-intercept (see "Materials and Methods").

Unpaired two-tailed *t*-tests reveal signif-

Table 2. Intraspecific variation in *face/eye*, *vertex/eye*, *face/vertex*, and CDI scores calculated for *E. aestuans* and *E. albibarbis*, as described by summary statistics (minimum, maximum, median, and mean  $\pm$  standard deviation).

<i>E. aestuans</i>	<i>n</i>	Face/Eye				Vertex/Eye			
		min	max	Median	Mean $\pm$ SD	min	max	Median	Mean $\pm$ SD
MWUSA, ♂♂	15	0.7037	0.9643	0.8281	0.8321 $\pm$ 0.0609	0.6049	0.8627	0.7077	0.7038 $\pm$ 0.0644
MWUSA, ♀♀	33	0.7471	0.9608	0.8302	0.8356 $\pm$ 0.0501	0.5977	0.8750	0.6957	0.7011 $\pm$ 0.0553
total	48	0.7037	0.9643	0.8292	0.8345 $\pm$ 0.0531	0.5977	0.8750	0.6992	0.7019 $\pm$ 0.0576
	<i>n</i>	Face/Vertex				CDI			
		min	max	Median	Mean $\pm$ SD	min	max	Median	Mean $\pm$ SD
MWUSA, ♂♂	15	1.1020	1.2292	1.1875	1.1843 $\pm$ 0.0352	0.0893	0.1579	0.1316	0.1283 $\pm$ 0.0206
MWUSA, ♀♀	33	1.1042	1.2745	1.1915	1.1941 $\pm$ 0.0433	0.0806	0.1892	0.1333	0.1345 $\pm$ 0.0255
total	48	1.1020	1.2745	1.1915	1.1910 $\pm$ 0.0408	0.0806	0.1872	0.1325	0.1326 $\pm$ 0.0241
<i>E. albibarbis</i>	<i>n</i>	Face/Eye				Vertex/Eye			
		min	max	Median	Mean $\pm$ SD	min	max	Median	Mean $\pm$ SD
MWUSA, ♂♂	30	0.8714	1.0508	0.9370	0.9347 $\pm$ 0.0344	0.8548	1.0702	0.9692	0.9446 $\pm$ 0.0744
MWUSA, ♀♀	21	0.8852	1.0678	0.9821	0.9707 $\pm$ 0.0589	0.8730	1.0526	0.9524	0.9518 $\pm$ 0.0492
BAJA, ♂♂	09	0.7746	0.9048	0.8333	0.8365 $\pm$ 0.0502	0.8169	1.0161	0.8983	0.9135 $\pm$ 0.0786
BAJA, ♀♀	16	0.8308	0.9298	0.8750	0.8770 $\pm$ 0.0290	0.8060	1.0385	0.9365	0.9295 $\pm$ 0.0540
CAMER, ♂♂	08	0.8065	0.8800	0.8489	0.8449 $\pm$ 0.0299	0.8448	0.9444	0.8880	0.8900 $\pm$ 0.0388
CAMER, ♀♀	04	0.8226	0.8889	0.8489	0.8523 $\pm$ 0.0302	0.8387	0.8704	0.8581	0.8563 $\pm$ 0.0140
SWUSA, ♂♂	09	0.7794	0.9038	0.8451	0.8372 $\pm$ 0.0381	0.8182	0.9423	0.8524	0.8697 $\pm$ 0.0433
SWUSA, ♀♀	05	0.8070	0.8730	0.8524	0.8451 $\pm$ 0.0250	0.8197	0.9048	0.8246	0.8483 $\pm$ 0.0307
total, ♂♂	56	0.7746	1.0508	0.9035	0.8904 $\pm$ 0.0602	0.8169	1.0702	0.9310	0.9236 $\pm$ 0.0610
total, ♀♀	46	0.8070	1.0678	0.8899	0.9142 $\pm$ 0.0670	0.8060	1.0526	0.9370	0.9277 $\pm$ 0.0638
total	102	0.7746	1.0678	0.8928	0.9011 $\pm$ 0.0642	0.8060	1.0702	0.9360	0.9255 $\pm$ 0.0620
	<i>n</i>	Face/Vertex				CDI			
		min	max	Median	Mean $\pm$ SD	min	max	Median	Mean $\pm$ SD
MWUSA, ♂♂	30	0.8841	1.0526	0.9845	0.9834 $\pm$ 0.0391	-0.1228	0.0469	-0.0146	-0.0171 $\pm$ 0.0387
MWUSA, ♀♀	21	0.9683	1.0508	1.0160	1.0113 $\pm$ 0.0207	-0.0308	0.0476	0.0153	0.0107 $\pm$ 0.0195
BAJA, ♂♂	09	0.8868	1.0000	0.8939	0.9180 $\pm$ 0.0476	-0.1129	0.0000	-0.1017	-0.0771 $\pm$ 0.0496
BAJA, ♀♀	16	0.8889	1.0370	0.9439	0.9452 $\pm$ 0.0357	-0.1154	0.0299	-0.0504	-0.0525 $\pm$ 0.0347
CAMER, ♂♂	08	0.9091	1.0200	0.9381	0.9502 $\pm$ 0.0355	-0.0806	0.0169	-0.0541	-0.0450 $\pm$ 0.0320
CAMER, ♀♀	04	0.9783	1.0213	0.9904	0.9951 $\pm$ 0.0200	-0.0185	0.0185	-0.0081	-0.0040 $\pm$ 0.0171
SWUSA, ♂♂	09	0.9138	1.0000	0.9630	0.9632 $\pm$ 0.0304	-0.0735	0.0000	-0.0303	-0.0325 $\pm$ 0.0271
SWUSA, ♀♀	05	0.9649	1.0400	0.9818	0.9971 $\pm$ 0.0315	-0.0317	0.0328	-0.0159	-0.0032 $\pm$ 0.0267
total, ♂♂	56	0.8841	1.0526	0.9753	0.9649 $\pm$ 0.0438	-0.1228	0.0469	-0.0227	-0.0033 $\pm$ 0.0418
total, ♀♀	46	0.8889	1.0508	0.9821	0.9859 $\pm$ 0.0404	-0.1154	0.0476	-0.0130	-0.0135 $\pm$ 0.0384
total	102	0.8841	1.0526	0.9818	0.9745 $\pm$ 0.0434	-0.1228	0.0476	-0.0161	-0.0242 $\pm$ 0.0413

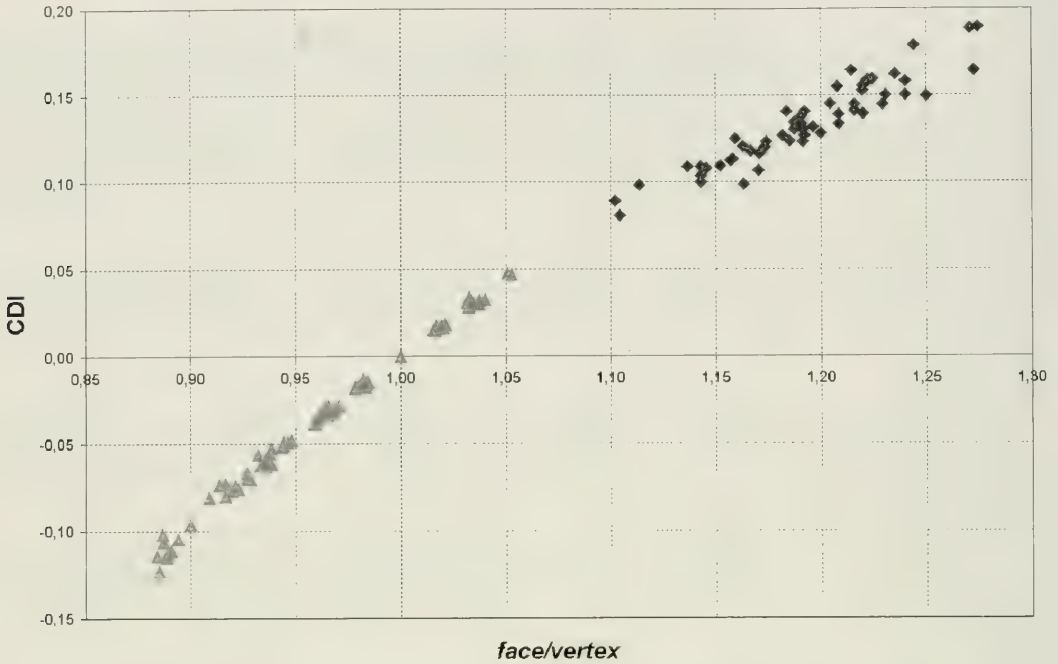


Fig. 2. Correlation plot for *face/eye* and CDI scores, showing separation of distributions and "Pattern 4" linear trends for *E. albibarbis* (triangles—lower scores) and *E. aestuans* (diamonds—higher scores).

icant differences between *E. albibarbis* and *E. aestuans* ( $P < 0.001$ ) and significant intraspecific differences for *E. albibarbis* (Table 3). Differences between males and females were not significant for *E. aestuans* ( $P > 0.413$ ) but significant between males and females of *E. albibarbis* in *face/vertex* scores ( $P = 0.014$ ) and nearly significant in *face/vertex* scores ( $P = 0.062$ ). Males and females from MWUSA constitute the largest geographic group of *E. albibarbis* specimens, and have a higher significant difference in *face/vertex* ( $P = 0.004$ ) and are significantly different in *face/eye* ( $P = 0.008$ ) and CDI scores ( $P = 0.003$ ). Significant differences between males and females in *face/vertex* scores were also detected for BAJA ( $P = 0.041$ ) and CAMER ( $P = 0.043$ ) groups and in CDI scores for the CAMER group ( $P = 0.040$ ). Summary statistics and correlation plots of *face/eye* and CDI scores show that scores for MWUSA *E. albibarbis* males extend farther into the realm of divergent eye scores (i.e., lower

*face/vertex* and CDI scores for males) whereas there is a complete overlap of scores for males and females of *E. aestuans* (Fig. 3, Table 3). More females than males have *face/vertex* scores greater than 1.0 ( $n_{\text{males}} = 14$ ,  $n_{\text{females}} = 18$ ), more males have *face/vertex* scores between 1.0 and 0.965 ( $n_{\text{males}} = 11$ ,  $n_{\text{females}} = 3$ ), and only males have scores below 0.965 ( $n_{\text{males}} = 5$ ,  $n_{\text{females}} = 0$ ).

Interspecific variation.—The four eye morphology variables identify outliers rather than discrete groups of *Efferia* species, and all but two *Efferia* group species (*T. interrupta* and *E. albibarbis*) have compound eyes that are closer at the vertex than at the frons (i.e., *face width* > *vertex width*) (Fig. 4, Table 4). The *face/vertex* ratio and CDI indicate divergence of the eyes at the vertex for *T. interrupta*, neither divergence nor convergence for *E. albibarbis*, and convergence for all other *Efferia* group species. The lowest *face/vertex* scores are recorded for *T. interrupta* (0.980) and *E. albibarbis*

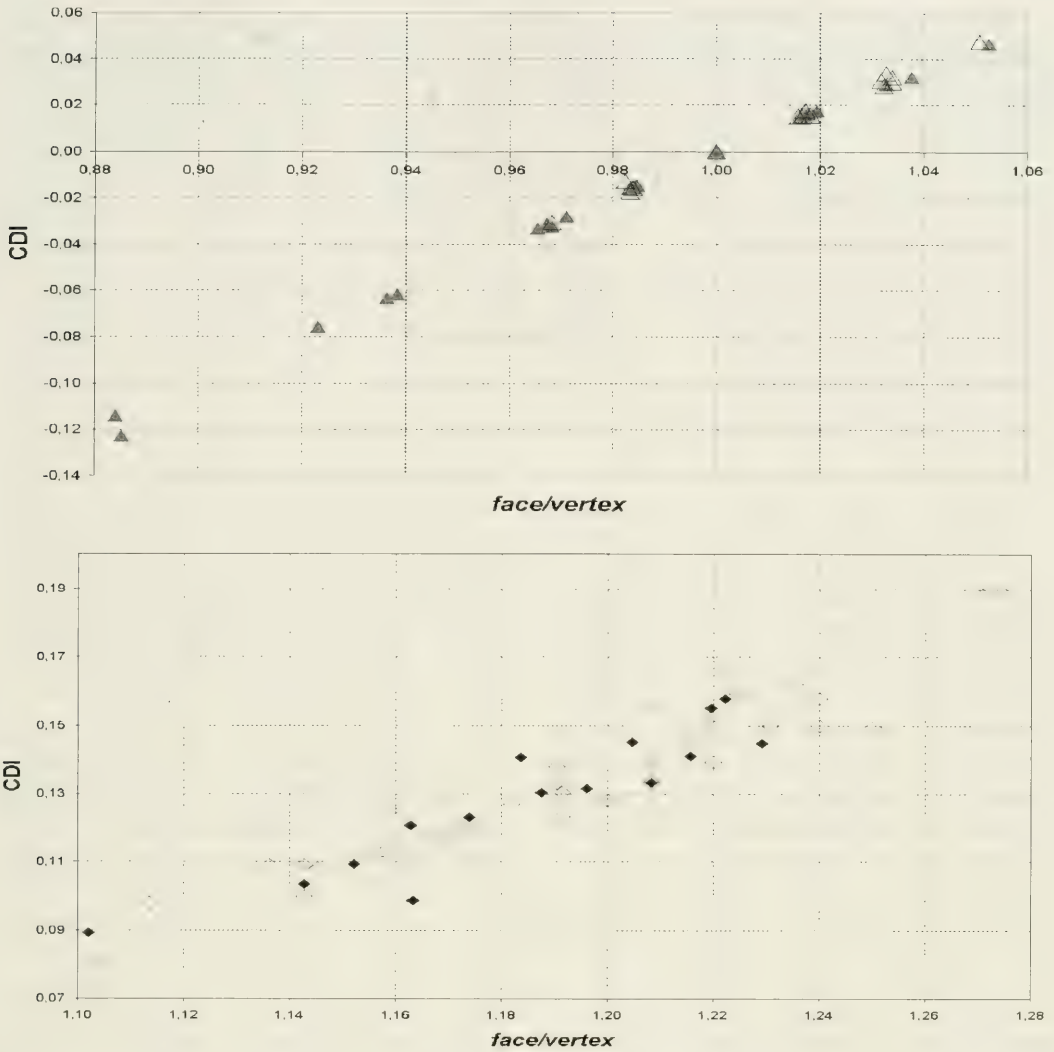


Fig. 3. Correlation plots of *face/eye* and CDI scores for MWUSA *E. albibarbis* (upper plot, triangles) and *E. aestuans* (lower plot, diamonds) comparing distributions of males (solid symbols) and females (open symbols), with lower scores for males than females in *E. albibarbis*.

(1.000); and the highest scores are observed for *E. leucomoma* (Williston) (1.500), *E. zonata* (Hine) (1.500), and *E. peralta* Wilcox (1.600), with *E. peralta* as an upper outlier among *Efferia* group species (Fig. 4). The lowest CDI scores were also obtained for *T. interrupta* (-0.0189) and *E. albibarbis* (0.000), but *E. leucomoma* has the highest CDI score (0.308) with *T. interrupta*, *E. albibarbis*, and *E. leucomoma* as outliers for the CDI (Fig. 4). The *face/vertex* and CDI scores for *E. albibarbis* and *E.*

*aestuans* include scores calculated from Wilcox (1966) measurements. There is, however, broad overlap in distributions of scores for the eight *Efferia* species groups in all eye morphology variables (Table 5), and the ranges of *face/vertex* and CDI scores for *E. albibarbis* and *E. aestuans* encompass scores for *T. interrupta* and 37 other *Efferia* species (Fig. 5).

The correlation plot for *Efferia* group species shows a linear relationship for *face/vertex* and CDI scores, and the slope of the



Table 3. Results ( $p$ -values) from unpaired two-tailed  $t$ -tests of *face/eye*, *vertex/eye*, *face/vertex*, and CDI scores; with comparisons between *E. aestuans* and *E. albibarbis*, between all males and females of *E. aestuans* and *E. albibarbis*, and between males and females of *E. albibarbis* grouped by geographic region. Significant differences between groups ( $\alpha = 0.05$ ) are indicated by asterisks (\*).

	Face/Eye	Vertex/Eye	Face/Vertex	CDI
<i>E. aestuans</i> v. <i>E. albibarbis</i>	<0.001*	<0.001*	<0.001*	<0.001*
<i>E. aestuans</i> v. <i>E. albibarbis</i> , ♂♂	<0.001*	<0.001*	<0.001*	<0.001*
<i>E. aestuans</i> v. <i>E. albibarbis</i> , ♀♀	<0.001*	<0.001*	<0.001*	<0.001*
<i>E. aestuans</i> , ♂♂ v. <i>E. aestuans</i> , ♀♀	0.835	0.882	0.576	0.413
<i>E. albibarbis</i> , ♂♂ v. <i>E. albibarbis</i> , ♀♀	0.062	0.741	0.014*	0.203
MWUSA, ♂♂ v. MWUSA, ♀♀	0.008*	0.695	0.004*	0.003*
BAJA, ♂♂ v. BAJA, ♀♀	0.017*	0.522	0.041*	0.158
CAMER, ♂♂ v. CAMER, ♀♀	0.695	0.130	0.043*	0.040*
SWUSA, ♂♂ v. SWUSA, ♀♀	0.687	0.351	0.072	0.075

regression line through the x-intercept with best fit to the data ( $y = 0.6227x - 0.625$ ,  $R^2 = 0.6996$ ) has a value lower than median (0.6739) and mean *vertex/eye* scores ( $0.6651 \pm 0.1209$ ) (Fig. 6). *Efferia* species with the best fit to this linear regression have *vertex/eye* scores that are closest to 0.6227 (*E. azteci*: 0.6000, *E. wilcoxi*: 0.6207, *E. latrunculata*: 0.600, *E. inflata*: 0.6000, *E. pilosa*: 0.6250, *E. kansensis*: 0.6000, and *E. leucocoma*: 0.6154) (Table 4). As seen in the regressions for *E. aes-*

*tians* and *E. albibarbis*, the correlation plot shows greater spread of observations with increasing distance from the x-intercept, and *vertex/eye* scores indicate a lack of proportionality of vertex and eye widths among *Efferia* group species.

#### DISCUSSION

Intraspecific variation and interspecific distinctions.—All four variables can be used to distinguish specimens of *E. albibarbis* from *E. aestuans*. The significant

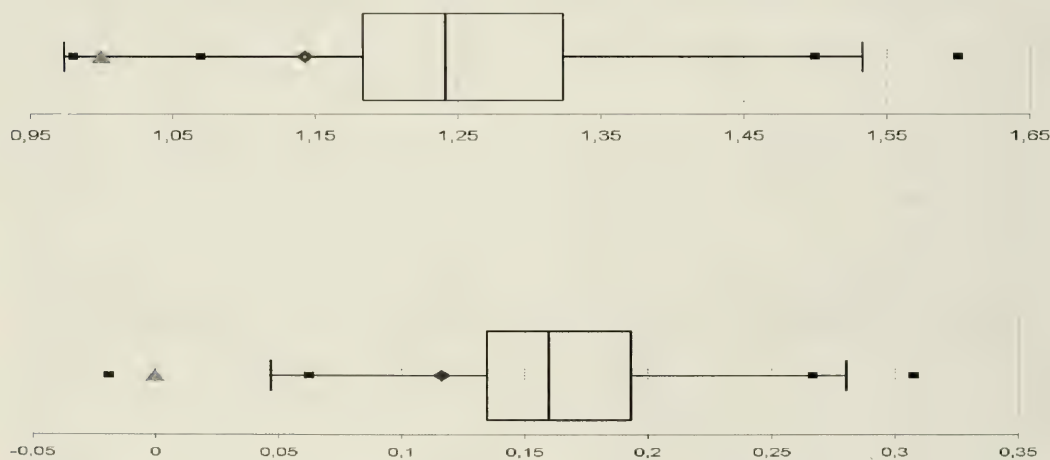


Fig. 4. Boxplots summarizing distributions of *face/vertex* (upper plot) and CDI (lower plot) scores, as listed for all species in Table 4. Symbols: *face/vertex*—*T. interrupta*, 0.980 (first square); *E. albibarbis*, 1.000, (triangle), *E. cana*, 1.070 (second square); *E. aestuans*, 1.143 (diamond); *E. leucocoma* and *E. zonata*, 1.500 (third square); and *E. peralta*, 1.600 (upper outlier, fourth square). Symbols: CDI—*T. interrupta*, -0.0189 (lower outlier, first square); *E. albibarbis*, 0.000 (lower outlier, triangle); *E. cana*, 0.062 (second square); *E. aestuans* (0.116, diamond); *E. peralta*, 0.267 (third square); and *E. leucocoma*, 0.308 (upper outlier, fourth square).

differences in eye morphology emphasize that *E. albibarbis* and *E. aestuans* are distinct species although the taxonomic status of these species is clearly established using a suite of traditionally used morphological characters (Wilcox 1966). Similarly, *E. albibarbis* and other species that are outliers in distributions of eye morphology scores can be diagnosed without reference to the variables defined in this study. These variables, however, are more informative descriptors of eye morphology than summaries of linear measurements (e.g., the average eye width for specimens examined), which lose diagnostic properties that are independent of specimen size. Further documentation of eye measurement ratios can improve the scope of current species diagnoses, but ratios should be selected based on their relevance to further taxonomic and biological investigations.

Intraspecific sexual differences.—The lower minimum, median, and mean *face/vertex*, CDI, and *face/eye* scores in male specimens of *E. albibarbis* indicate differences in eye morphology between males and females. Significant sexual differences were detected in *face/vertex*, CDI, and *face/eye* scores, indicating that males have either a narrower face or broader vertex and eye in comparison to females. The correlation between face and vertex widths for males of *E. albibarbis* indicates that face and vertex widths do not increase arithmetically as face and vertex widths for *E. albibarbis* females or for either sex of *E. aestuans*. Moderate variation in *vertex/eye* scores was observed for *E. albibarbis* and *E. aestuans*, and there is no significant difference in means of *vertex/eye* scores between males and females MWUSA specimens ( $P = 0.695$ ) or in comparisons of all *E. albibarbis* specimens ( $P = 0.741$ ) (Table 3). Males and females of *E. aestuans*, in contrast, are not significantly different in scores for any of the four eye morphology variables ( $P \geq 0.413$ ) despite a lack of proportional change in eye measurements (Table 3).

Lower *face/vertex*, CDI, and *face/eye*

scores are due to larger vertex and eye widths in males of *E. albibarbis* rather than narrower face widths. Face width and eye widths are related by a shared endpoint on the eye margin (Fig. 1), and a narrower face width that is not complemented by a larger eye width would result in sexual differences in ratios of overall head width (face width + eye width) to vertex width as in *face/vertex* scores. To investigate this possibility, two tailed *t*-tests for *(face+eye)/vertex* scores were performed. A lack of significant difference in *(face+eye)/vertex* scores between males and females from MWUSA ( $P = 0.334$ ) or all *E. albibarbis* specimens ( $P = 0.186$ ) shows that lower scores for eye divergence variables in males correspond to increases in both eye and vertex widths. An arithmetic increase in both vertex and eye width explains the lack of significant difference between males and females in *vertex/eye* scores. Furthermore, a positive correlation between face and eye widths in *E. albibarbis* demonstrates that eye width increases with increasing face widths, and males have a stronger positive correlation in vertex and eye widths than females. The correlations between *face/vertex* and CDI scores also indicate that face, eye, and vertex measurements increase arithmetically: the fit to a linear regression is not due to proportional changes in *vertex/eye* scores.

Sexual differences in eye morphology have not been documented in previous studies of Asilidae and suggest that directional selection in *E. albibarbis* may have shifted *face/vertex*, CDI, and *face/eye* scores to lower means in males. The distribution of *face/vertex* and CDI scores for fly species with holoptic males would be bimodal and non-overlapping between males and females. Eye morphology in robber fly species is considered identical between males and females, and the predicted distribution of *face/vertex* and CDI scores would be unimodal, with complete overlap and identical means for male and female distributions. In *E. albibarbis*, however, males have lower median and mean scores than females, with

Table 4. Scores for *face/eye* (*f/eye*), *vertex/eye* (*v/eye*), *face/vertex* (*f/v*), and CDI calculated from measurements reported in Wilcox (1966) for North American *Efferia* species (and \**Triorla interrupta*).

Species	<i>f/eye</i>	<i>v/eye</i>	<i>f/v</i>	CDI
<i>aestuans</i>	0.9302	0.8140	1.1429	0.1163
<i>albibarbis</i>	0.8333	0.8333	1.0000	0.0000
<i>antiochi</i>	0.8889	0.7556	1.1765	0.1333
<i>apache</i>	0.8605	0.7209	1.1935	0.1395
<i>apicalis</i>	0.7660	0.5532	1.3846	0.2128
<i>argentifrons</i>	0.8776	0.7551	1.1622	0.1224
<i>argyrosoma</i>	0.8889	0.7333	1.2121	0.1556
<i>arida</i>	0.9091	0.7636	1.1905	0.1455
<i>armata</i>	0.9063	0.7500	1.2083	0.1563
<i>aurimystaceus</i>	0.8684	0.6316	1.3750	0.2368
<i>auripila</i>	1.0000	0.9184	1.0889	0.0816
<i>azteci</i>	0.7143	0.6000	1.1905	0.1143
<i>basingeri</i>	0.8039	0.6863	1.1714	0.1176
<i>basini</i>	0.9091	0.7500	1.2121	0.1591
<i>beameri</i>	0.7368	0.5789	1.2727	0.1622
<i>belfragei</i>	0.8649	0.7027	1.2308	0.1622
<i>benedicti</i>	0.8261	0.6522	1.2667	0.1739
<i>bexarensis</i>	0.9592	0.7143	1.3429	0.2449
<i>bicaudata</i>	0.8776	0.7959	1.1026	0.0816
<i>bicolor</i>	0.7879	0.5303	1.4857	0.2576
<i>bryanti</i>	0.8261	0.6739	1.2258	0.1522
<i>cabeza</i>	0.8235	0.7059	1.1667	0.1176
<i>caliente</i>	0.8500	0.7000	1.2143	0.1500
<i>californica</i>	0.8333	0.6875	1.2121	0.1458
<i>cana</i>	0.9583	0.8958	1.0698	0.0625
<i>canella</i>	0.7200	0.5800	1.2414	0.1400
<i>clementi</i>	0.7778	0.5556	1.4000	0.2222
<i>coquilletti</i>	0.7429	0.6286	1.1818	0.1143
<i>costalis</i>	0.7209	0.5349	1.3478	0.1860
<i>coulei</i>	0.9118	0.8235	1.1071	0.0882
<i>cressoni</i>	0.6667	0.4615	1.4444	0.2051
<i>davisi</i>	0.8333	0.6667	1.2500	0.1667
<i>deserti</i>	0.8222	0.7556	1.0882	0.0667
<i>ehrenbergi</i>	0.6757	0.5405	1.2500	0.1351
<i>femoratus</i>	0.8167	0.6333	1.2895	0.1833
<i>frewingi</i>	0.8837	0.6977	1.2667	0.1860
<i>gila</i>	0.8824	0.7451	1.1842	0.1373
<i>halli</i>	0.8780	0.7805	1.1250	0.0976
<i>helenae</i>	0.9434	0.7170	1.3158	0.2264
<i>inflata</i>	0.7917	0.6250	1.2667	0.1667
<i>interrupta*</i>	0.9434	0.9623	0.9804	-0.0189
<i>jubata</i>	0.7091	0.5091	1.3929	0.2000
<i>kansensis</i>	0.8500	0.6000	1.4167	0.2500
<i>kelloggi</i>	0.9200	0.7600	1.2105	0.1600
<i>latruncula</i>	0.7556	0.6000	1.2593	0.1556
<i>leucocoma</i>	0.9231	0.6154	1.5000	0.3077
<i>luma</i>	0.8222	0.7333	1.1212	0.0889
<i>mortensoni</i>	0.9592	0.8163	1.1750	0.1429
<i>nemoralis</i>	1.0638	0.8723	1.2195	0.1915
<i>neoinflata</i>	0.8654	0.6154	1.4063	0.2500
<i>ordwayae</i>	0.7750	0.6000	1.2917	0.1750
<i>pallidula</i>	0.8723	0.7021	1.2424	0.1702
<i>parkeri</i>	0.7949	0.6410	1.2400	0.1538

Table 4. Continued.

Species	<i>f/eye</i>	<i>v/eye</i>	<i>f/v</i>	CDI
<i>peralta</i>	0.7111	0.4444	1.6000	0.2667
<i>pilosa</i>	0.8000	0.6000	1.3333	0.2000
<i>pinali</i>	0.9200	0.7000	1.3143	0.2200
<i>plena</i>	0.9677	0.8065	1.2000	0.1613
<i>prairiensis</i>	1.0952	0.9524	1.1500	0.1429
<i>producta</i>	0.6923	0.5128	1.3500	0.1795
<i>prolifca</i>	0.6667	0.5333	1.2500	0.1333
<i>rapax</i>	0.8077	0.5769	1.4000	0.2308
<i>setigera</i>	0.7200	0.5000	1.4400	0.2200
<i>similis</i>	0.7031	0.5469	1.2857	0.1563
<i>spiniiventris</i>	0.7419	0.5806	1.2778	0.1613
<i>staminea</i>	0.8571	0.6905	1.2414	0.1667
<i>subcuprea</i>	0.7442	0.5814	1.2800	0.1628
<i>tabescens</i>	0.7333	0.5556	1.3200	0.1778
<i>tagax</i>	0.7353	0.5588	1.3158	0.1765
<i>texana</i>	0.9091	0.7636	1.1905	0.1455
<i>tolandi</i>	0.8333	0.7500	1.1111	0.0833
<i>truncata</i>	0.8864	0.7500	1.1818	0.1364
<i>tuberculata</i>	0.7632	0.5263	1.4500	0.2368
<i>tucsoni</i>	0.6341	0.4390	1.4444	0.1951
<i>utahensis</i>	0.8824	0.6863	1.2857	0.1961
<i>varipes</i>	0.9583	0.7917	1.2105	0.1667
<i>vertebrata</i>	0.6538	0.4615	1.4167	0.1923
<i>willcoxi</i>	0.7586	0.6207	1.2222	0.1379
<i>willistoni</i>	0.8077	0.5769	1.4000	0.2308
<i>yermo</i>	0.8000	0.7250	1.1034	0.0750
<i>yuma</i>	0.6250	0.5208	1.2000	0.1042
<i>zonata</i>	0.6667	0.4444	1.5000	0.2222

*face/vertex* and CDI scores for females falling completely within the upper range of male scores. The observed distribution for *E. albibarbis* may indicate a morphological shift in males toward larger vertex and eye widths related if there has been selective pressure that favors larger eyes in males (or smaller eyes in females). Results from this study suggest that the degree of sexual differences in eye morphology varies among populations of *E. albibarbis*, allowing the effect of various natural selective regimes on eye morphology to be examined.

Habitat differences among populations of *E. albibarbis* have not been described, but the widespread distribution of this species, and high variation in eye morphology in females and males relative to *E. aestuans*, suggest that adaptation to local environ-

ments is possible. Specimens of *E. albibarbis* from BAJA have lower *face/vertex* and CDI means than for the MWUSA group, but extensive sampling is needed to characterize geographic groups and populations of this species. A simple mode of mate interception after short flights (similar to flight observed for prey capture) and the lack of courtship displays has been noted for *E. albibarbis* and most *Efferia* species (Lavigne 2002), and the same selective advantage in mate acquisition assumed for holoptic males in other groups of Diptera can be invoked concerning the larger vertex and eye widths in *E. albibarbis* males. Optimization of eye dimensions for successful prey capture and predator avoidance is likely to constrain levels of variation within and among robber fly species, with enhanced

Table 5. Interspecific variation in *face/eye*, *vertex/eye*, *face/vertex*, and CDI scores calculated from measurements reported in Wilcox (1966) for species groups of *Efferia*, as described by summary statistics (minimum, maximum, median, and mean  $\pm$  standard deviation). \*Scores for *T. interrupta* are presented with minimum or maximum scores for species groups.

Spp. Group	n	Face/Eye				Vertex/Eye			
		min	max	Median	Mean $\pm$ SD	min	max	Median	Mean $\pm$ SD
Aestuans	08	0.7333	0.9302	0.8333	0.8208 $\pm$ 0.0705	0.5532	0.8140	0.6158	0.6337 $\pm$ 0.0878
Albibarbis	09	0.6538	0.9231	0.7353	0.7690 $\pm$ 0.0998	0.4444	0.8333	0.5469	0.5761 $\pm$ 0.1365
Anomala	07	0.7143	0.8889	0.8333	0.8350 $\pm$ 0.0603	0.6000	0.7805	0.7333	0.7079 $\pm$ 0.0633
Arida	06	0.8039	0.9200	0.8848	0.8731 $\pm$ 0.0480	0.6863	0.8235	0.7355	0.7407 $\pm$ 0.0500
Carinata	09	0.6667	0.8500	0.7442	0.7440 $\pm$ 0.0613	0.4615	0.7000	0.5769	0.5664 $\pm$ 0.0678
Poginias	07	0.8235	0.9592	0.8837	0.8985 $\pm$ 0.0460	0.6863	0.8163	0.7170	0.7399 $\pm$ 0.0512
Staminea	29	0.6250	1.0952	0.8571	0.8567 $\pm$ 0.1078	0.5208	0.9524	0.7021	0.7042 $\pm$ 0.1140
Tuberculata	05	0.6341	0.7632	0.7200	0.7103 $\pm$ 0.0500	0.4390	0.5806	0.5128	0.5118 $\pm$ 0.0510
<i>T. interrupta</i> *	01		0.9434				0.9623		
Total	81	0.6250	1.0952	0.8261	0.8259 $\pm$ 0.0984	0.4390	0.9623	0.6739	0.6651 $\pm$ 0.1209
Spp. Group	n	Face/Vertex				CDI			
		min	max	Median	Mean $\pm$ SD	min	max	Median	Mean $\pm$ SD
Aestuans	08	1.1429	1.4167	1.3047	1.3047 $\pm$ 0.0902	0.1163	0.2500	0.1806	0.1871 $\pm$ 0.0442
Albibarbis	09	1.0000	1.6000	1.4167	1.3680 $\pm$ 0.1855	0.0000	0.3077	0.1923	0.1928 $\pm$ 0.0893
Anomala	07	1.1212	1.2500	1.1842	1.1819 $\pm$ 0.0476	0.0889	0.1667	0.1333	0.1272 $\pm$ 0.0284
Arida	06	1.1071	1.3143	1.1810	1.1813 $\pm$ 0.0754	0.0833	0.2200	0.1286	0.1324 $\pm$ 0.0499
Carinata	09	1.2143	1.4444	1.2917	1.3200 $\pm$ 0.0792	0.1333	0.2308	0.1750	0.1776 $\pm$ 0.0308
Poginias	07	1.1026	1.3158	1.2105	1.2176 $\pm$ 0.0757	0.0816	0.2264	0.1600	0.1587 $\pm$ 0.0493
Staminea	29	1.0698	1.4063	1.2121	1.2254 $\pm$ 0.0881	0.0625	0.2500	0.1538	0.1525 $\pm$ 0.0488
Tuberculata	05	1.2778	1.4500	1.4400	1.3924 $\pm$ 0.0762	0.1613	0.2368	0.1951	0.1985 $\pm$ 0.0304
<i>T. interrupta</i> *	01	0.9804				-0.0189			
Total	81	0.9804	1.6000	1.2414	1.2591 $\pm$ 0.1197	-0.0189	0.3077	0.1600	0.1608 $\pm$ 0.0569

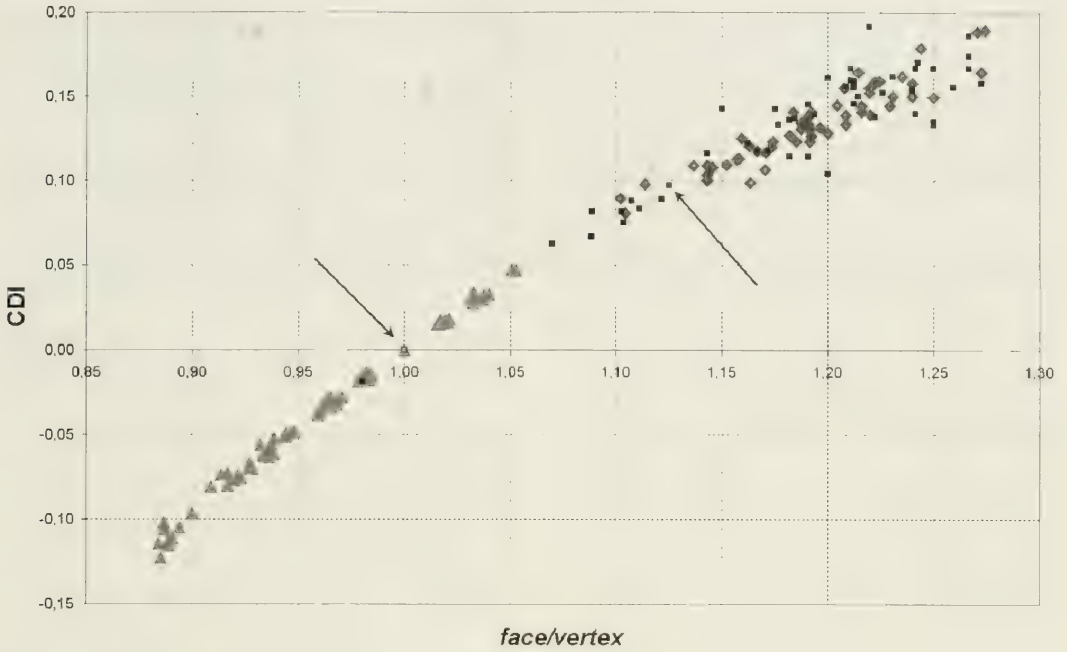


Fig. 5. Correlation plot for *face/eye* and CDI scores, showing overlap between single exemplars of *Efferia* species (small squares, data in Table 4) and intraspecific variation in *E. albibarbis* and *E. aestuans* (see Fig. 2). Arrows indicate positions of Wilcox (1966) exemplars for *E. albibarbis* (lower left) and *E. aestuans* (upper right).

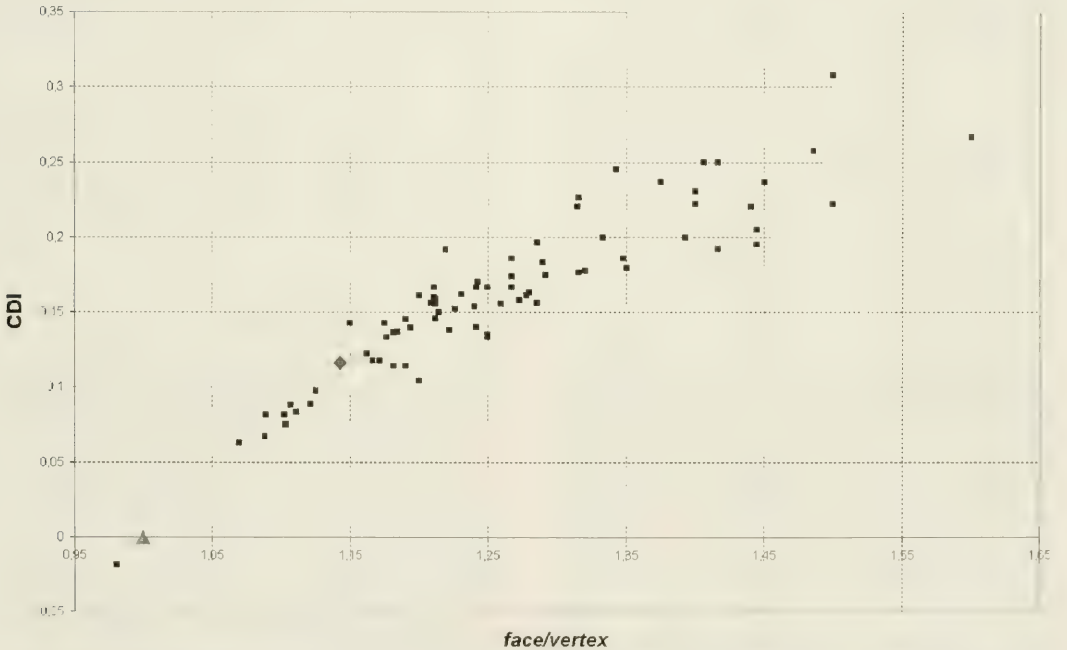


Fig. 6. Correlation plot of *face/vertex* and CDI scores for all *Efferia* group species (see Table 4) (triangle = *E. albibarbis*, diamond = *E. aestuans*).

mate acquisition promoting larger vertex and eye widths relative to face width in males of *E. albibarbis*.

Interspecific differences.—Single specimens are insufficient for robust comparisons between most *Efferia* species based on intraspecific variation in *E. aestuans* and *E. albibarbis*, but these scores suggest that certain species have notable eye morphologies. As noted, *face/vertex* and CDI scores show that *T. interrupta* and *E. albibarbis* are lower outliers and *E. leucocoma* and *E. peralta* are upper outliers among *Efferia* group species. The taxonomic status of *Efferia* species groups has not been confirmed or clarified by eye morphology variables, with scores resulting in continuous distributions. Group circumscriptions, however, have substantial ranges of interspecific variation in eye morphology based on Wilcox (1966) measurements. *Efferia* species exemplars can be distinguished by *face/vertex* and CDI scores although scores for nearly half of the *Efferia* species fall within the range of intraspecific variation in *E. aestuans* and do not allow *T. interrupta* to be distinguished from *E. albibarbis* specimens. Furthermore, scores for *E. albibarbis* and *E. aestuans* specimens vary considerably around the scores calculated for single exemplars of these species. Additional intraspecific sampling will reveal whether levels of variation for *Efferia* species are similar to *E. albibarbis* and *E. aestuans*, and should allow differences in eye morphology among *Efferia* species to be identified and compared.

Eye morphology variables identified in this study can be used to investigate evolutionary changes within or among monophyletic groups and ecological guilds. Differences in habitat preferences between *E. aestuans* and *E. albibarbis* may explain the lack of sexual dimorphism in *E. aestuans*; *E. albibarbis* is found primarily on or near the ground and often in sandy areas whereas *E. aestuans* is primarily arboreal and found in forested habitats (Bullington and Lavigne 1984). Ecological classifications

for Asilidae proposed by Londt (1994) would place *E. aestuans* in Category 6, “trees,” and *E. albibarbis* in Category 1, “ground,” and *Efferia* species have been recorded from these and other the four ecological categories. Further data on eye morphology may reveal correlations with “hunting areas” for species similar to correlations noted between ovipositor morphology and oviposition sites (Londt 1994). Two groups of *Efferia* species that are strongly supported as monophyletic, based on the laterally compressed mesonotum with a medial crest of macrosetae (the *Carinata* Group) and tubercle-like projections from the abdominal sternites (the *Tuberculata* group), are not differentiable based on exemplar scores, but differences in eye morphology scores among species suggest that trends in eye morphology variation can be identified by variables defined in this study. The ecological diversity in *Efferia* provides an informative context for investigating sexual dimorphism in *E. albibarbis* and testing evolutionary hypotheses for monophyletic groups in *Efferia*; these studies would promote a deeper understanding of robber fly diversity.

#### ACKNOWLEDGMENTS

We thank Eric Fisher and Aubrey Scarbrough for improving the text of this paper as well as Donald Webb and the INHS for technical support during initial data collection.

#### LITERATURE CITED

- Artigas, J. N. and N. Papavero. 1997. The American genera of Asilidae (Diptera): keys for identification with an atlas of female spermathecae and other morphological details. IX.2. Subfamily Asilinae Leach—*Efferia* group, with the proposal of five new genera and a catalogue of the neotropical species. *Arquivos de Zoologia* 34(3): 65–95.
- Bullington, S. W. and R. J. Lavigne. 1984. Description and habitat of *Efferia kondratieffi* sp. nov. with notes on *Efferia aestuans* (L.) (Diptera: Asilidae). *Annals of the Entomological Society of America* 77: 404–413.
- Buschbeck, E. K. and N. J. Strausfeld. 1996. Visual motion-detection circuits in flies: small-field retin-

- optic elements responding to motion are evolutionarily conserved across taxa. *The Journal of Neuroscience* 16(15): 4563–4578.
- . 1997. The relevance of neural architecture to visual performance: phylogenetic conservation and variation in dipteran visual systems. *The Journal of Comparative Neurology* 383: 282–304.
- Fisher, E. M. and H. A. Hespeneide. 1992. Taxonomy and biology of Central American robber flies with an illustrated key to the genera (Diptera, Asilidae), pp. 610–631. *In* Quintero Arias, D. and A. Aiello, eds. *Insects of Panama and Meso-America: Selected Studies*. Oxford University Press, Oxford.
- Hine, J. S. 1919. Robber flies of the genus *Erax*. *Annals of the Entomological Society of America* 12(2): 103–157.
- Hull, F. M. 1962. Robber flies of the world. The genera of the family Asilidae. *Bulletin of the United States National Museum* 224(1, 2): 1–907.
- Lavigne, R. J. 2002. Evolution of courtship behavior among the Asilidae (Diptera), with a review of courtship and mating. *Studia Dipterologica* 9(2): 703–742.
- Lehr, P. A. 1988. Family Asilidae, pp. 197–326. *In* Soos, A. and L. Papp, eds. *Catalogue of Palaearctic Diptera*, Vol. 5, Akadémiai Kiadó, Budapest. 446 pp.
- Londt, J. G. H. 1994. Afrotropical Asilidae (Diptera) 26. Ethological observations, and a possible ecological classification based on habits. *Annals of the Natal Museum* 35: 97–122.
- Majer, J. M. 1997. 2.38. European Asilidae, pp. 549–566. *In* Papp, L. and B. Darvas, eds. *Contribution to a Manual of Palaearctic Diptera (with Special Reference to Flies of Economic Importance)*, Vol. 2 [Nematocera and Lower Brachycera], Science Herald, Budapest, 566 pp.
- Martin, C. H. and N. Papavero. 1970. 35b. Family Asilidae, pp. 1–139. *In* A Catalogue of the Diptera of the Americas South of United States. Museu de Zoologia, Universidade de São Paulo.
- McAlpine, J. F. 1981. Morphology and Terminology—Adults, pp. 9–63 *In* McAlpine, J. F., B.V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood, eds. *Manual of Nearctic Diptera*. Vol. 1. Monograph No. 27, Research Branch Agriculture Canada, Ottawa, 674 pp.
- Wilcox, J. 1966. *Efferia* Coquillett in America north of Mexico (Diptera: Asilidae). *Proceedings of the California Academy of Science* 34: 85–234.
- Wood, G. C. 1981. Asilidae, pp. 549–573. *In* McAlpine, J. F., B.V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood, eds. *Manual of Nearctic Diptera*, Vol. 1. Monograph No. 27, Research Branch Agriculture Canada, Ottawa, 674 pp.
- Yeates, D. K. 1994. The cladistics and classification of the Bombyliidae (Diptera: Asilioidea). *Bulletin of the American Museum of Natural History* 219: 1–191.